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BIOLOGY OF *ANAEA RYPHEA* (NYMPHALIDAE) IN CAMPINAS, BRAZIL

ASTRID CALDAS
Departamento de Biologia Animal e Vegetal—IB,
Universidade do Estado do Rio de Janeiro,
Rio de Janeiro, RJ 20550-013, Brazil

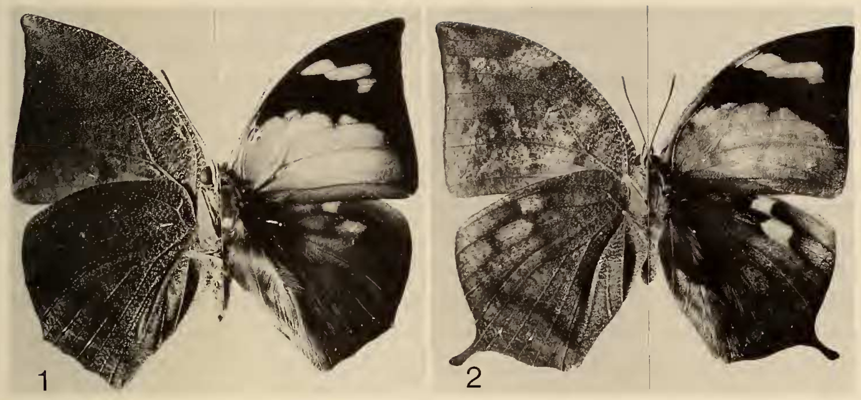
ABSTRACT. *Anaea ryphea* uses *Croton floribundus* (Euphorbiacae) as its main larval food plant at Campinas, Brazil. Weekly censuses of the immature stages of *A. ryphea* were conducted from September 1988 to August 1989. Adults and larvae were found only from December through May. Females usually laid one egg per leaf and exhibited no plant height preference. Within individuals plants, most eggs were laid on the intermediate leaves; they were rare on the lowest and absent on the apical, new leaves. The complete life cycle in the field lasts 50 to 60 days. The pattern of development in *A. ryphea* is similar to that described for 5 other species of *Anaea*. The early stages resemble closely those described for *A. eurypyle*, which also uses a species of *Croton* as its larval food plant in El Salvador.

Additional key words: *Hypna clytemnestra*, life cycle, *Memphis*, *Croton*, Euphorbiaceae.

The genus *Anaea* Hübner includes most of the Neotropical Charaxinae, although use of the generic name varies considerably among authors. Comstock (1961) assigned to *Anaea* the species now considered members of the *Anaea troglodyta* group. He used *Memphis* Hübner, formerly described as a generic name, as a subgenus for most of the other species of *Anaea*, including the blue species and *A. ryphea* (Cramer). Rydon (1971) subdivided the group further, describing *Fountainea*, into which he transferred *ryphea*. Although the most recent treatment of the group (Descimon 1986) recognizes *Anaea* as distinct from *Fountainea*, other authors (e.g., DeVries 1987) include *Fountainea* species in *Memphis*. According to Hemming (1967), *Anaea* has priority, leaving *Memphis* a synonym.

During the last ten years, *Anaea andria* Scudder has been the subject of several studies, and its biology is now well known. It uses *Croton capitatus* (Euphorbiaceae) as its primary larval food plant in North America (Riley 1981, 1988, 1989). The life cycles of other species of *Anaea* have been reported by Muyshondt (1973, 1974a, 1974b, 1975a, 1975b); however, the early stages of *A. ryphea* have remained unknown. DeVries (1987) reported *Anaea ryphea* from Mexico to the Amazon Basin, but it has become evident that its distribution is wider than previously thought. In southern Brazil it uses *Croton floribundus* Spreng (Euphorbiaceae) as its primary larval food plant (Caldas 1991).

Anaea ryphea is sexually dimorphic: males are smaller and usually lack the tail-like expansion of the hindwing (Figs. 1 & 2). Males are bright orange, red, and purple, with blue distal bars on the forewing cells.



FIGS. 1–2. Ventral (left) and dorsal (right) views of adult *Anaea ryphea*. **1**, male. **2**, female.

Females always have the hindwing expansion ("tail"), dark brown bars on the forewing cells, and yellow and orange as the dominant colors on both wings. The species is found in tropical and subtropical forests, where it can be seen in rapid flight or perched on urine, feces, and rotten fruits. Herein I describe the life cycle of *A. ryphea* from southeastern Brazil.

STUDY SITE AND METHODS

This study was conducted in the Santa Genebra Reserve, Campinas, São Paulo, Brazil (22°54'S, 47°05'W, elevation 650 m). The reserve includes 2,517,759 m^2 of disturbed subtropical semi-deciduous forest. Mean monthly temperature varies from 18°C to 29°C, with daily fluctuations of as much as 20°C from July to September. The dry season lasts from May through September. The rainy season may start with light rainfall or with heavy "summer storms." Frosts are rare, but may occur from July to September. Although the study was conducted from September 1988 through April 1991, the data presented here refer only to the first wet season, from December 1988 to May 1989.

I visited the reserve once a week from September 1988 through January 1989, then twice a week until mid-February. From then on, visits were more frequent, increasing to every other day until late April 1989, when they became weekly again.

Croton floribundus is a lactescent plant that can be either a small shrub or a tall tree, depending on its age and environmental conditions. The smallest plant found was only 20 cm tall, while the largest was more than 4 m. The leaves are alternate, stipulate, and grayish green.

Leaf size depends on plant height: 10 cm long on plants up to 2 m tall and 20 cm long on taller plants. The inflorescences are monoecious, with male flowers terminal. At the study site, flowers were seen during December. Other species of *Croton* are recorded as food plants for species of Nymphalidae (DeVries 1987) and Riodinidae (DeVries 1988). *Croton floribundus* is common in the Santa Genebra Reserve, in both sunny and shaded areas, as solitary individuals or in patches. It grows mostly along the edges of trails and is rare in the middle of the forest. The soil along the trails is mostly clay, and during the dry season the plants seem to resist desiccation. From May on, plants begin to dry out, sometimes being reduced to no more than a woody stem that puts out new leaves the next wet season. During the rainy season, the soil maintains a high water content. Along the reserve's central road (1,160 m long), I found 186 plants. All were mapped and marked for use in this study.

During each visit I checked all leaves for larvae on the 186 marked plants. Eggs were difficult to detect, so exact numbers were not known until the following season. Twenty eggs were collected and taken into the laboratory. These eggs were the source of hatching time observations. In the field, each leaf with a larva was individually numbered because larvae stay on the same leaf most of the time. All larvae were measured and identified as to instar. Their height from the ground and the general aspect of the leaf were noted. With this methodology I was able to (1) follow the growth of every individual, (2) determine the duration of each instar in the field, and (3) assess mortality for each instar.

RESULTS AND DISCUSSION

Oviposition

Anaea ryphea eggs are laid singly and usually one per leaf, in the central third of the under surface. Rarely, two or three eggs are laid. A similar oviposition pattern was described by Ramos (1984) for *Anaea troglodyta borinquenalis* and by Muyshondt (1975b) for *Anaea* (*Memphis*) *pithyusa*. Females fly around the plant, inspecting leaves quickly before ovipositing. I could not tell whether eggs laid on the same leaf came from the same female. Placing one egg per leaf could eliminate competition during the early instars, when larvae have restricted movement. In Colón Province, Republic of Panama, 1991, while studying the same species, I saw females placing more than one egg on the same leaf of *Croton billbergianus*, although not sequentially. In each of the three cases observed, the female flew from one leaf to another, ovipositing on acceptable leaves, eventually returning to oviposit on a leaf she already had used.

There was no plant height preference for oviposition among the 186 marked plants. All instars were found between 15 cm and 2 m above the ground, on short or tall plants. I did not include plants taller than 2 m in this study owing to the difficulty in reaching high leaves, but even on those, I could see active larvae when they were present. Within the same plant, though, larvae were found mostly on intermediate leaves, never on the apical ones, and rarely on the lower (older) ones. This distribution seems to be related to the age of the leaves, not to their height from the ground.

Development and Behavior

After eclosion larvae eat the egg shell and move toward the apex of the leaf where they begin to feed on both sides of the midvein, which when exposed becomes their resting place. This behavior, common in Nymphalidae, also is considered common for other *Anaea* species (Muyshondt 1974a). Ramos (1984) reported that larvae of *A. troglodyta borinquenalis* build a perching place from the tip instead of exposing the midvein first. When not feeding, *A. ryphea* larvae remain on this vein facing the apex, grasping the vein with both thoracic and abdominal legs. It is rare to see a larva start feeding on another part of the leaf, but when this happens, a lateral vein is chosen and used in the same manner. In either case, an individual may add fecula ("frass chain") to the vein, perhaps to strengthen it. Fecula is added mostly when the vein is thin, whether it is a lateral or central one. It also may be used to extend the vein beyond its natural length.

From the third instar on, *A. ryphea* larvae may roll the leaf to form a tubular shelter, holding it closed with silk, although this behavior usually is observed from fourth instar on. They begin by laying silk over the entire area of leaf that is to be rolled. As they add to and strengthen the threads, the leaf begins to curve and roll itself into a tube. Normally, the apical portion of the leaf is used to construct the shelter. If the leaf is damaged by some external event such as bird attack or herbivores, the larva may move to another leaf. Change of leaf does not necessarily follow any special rule, and I have observed larvae moving to new and old leaves, above or below the original one. The tube is open at both ends, but the opening that faces the base of the leaf is the larger of the two and is used by the larvae as the entrance and exit. The smaller opening is used to dispose of fecula. In order to enter the tube, the larva approaches close to opening, then makes a u-turn and backs into the shelter.

I did not measure leaf consumption, but observations show that larvae usually feed on the same leaf through the third instar, reducing it to one-half or one-third its original size. From third instar on, feeding increases noticeably. Larvae can move to another leaf and build a new tube if the first leaf is consumed before pupation, but that rarely was seen. More commonly they visit another leaf just to eat, then return to the old leaf where the shelter is kept (they never eat the roll). Feeding takes place mainly from dusk to dark, as do molting and pupation. When not eating, larvae remain on the midvein or inside the tube. During the last instar, the larva abandons the plant and searches for a suitable place to pupate.

Early Stages

Egg (Fig. 3). Approximately 1 mm in diameter (n = 10). Spherical, with small depression on top (micropyle end), greenish white, with no conspicuous sculpturing. Duration 5–6 days.

First Instar (Fig. 5). Length 1.5–8.0 mm (n = 1161). Head brown with dark brown spots, lighter near foramen; epicranial suture complete, well marked. Body eruciform, hazel, darker posteriorly. Duration approximately 6 days (n = 278).

Second Instar (Fig. 4). Length 5–14 mm (n = 598). Head light brown with three dark stripes on each side; frons with central dark stripe; pair of small scoli (each with two setae) on vertex, scattered chalazae restricted to sides of head. Body pale greenish brown with pale spots throughout, slightly enlarged on second abdominal segment. Duration approximately 6 days (n = 155).

Third Instar (Fig. 6). Length 8–20 mm (n = 308). Head similar to that of second instar, but with a series of dark spots between the three dark stripes of the epicranium, also some dark dots around the foramen; scoli larger than on second instar, with more chalazae. Body green, except second, fifth, and seventh abdominal tergi, which are brown; second abdominal segment enlarged, forming a small dorsal hump. Duration approximately 7 days (n = 105).

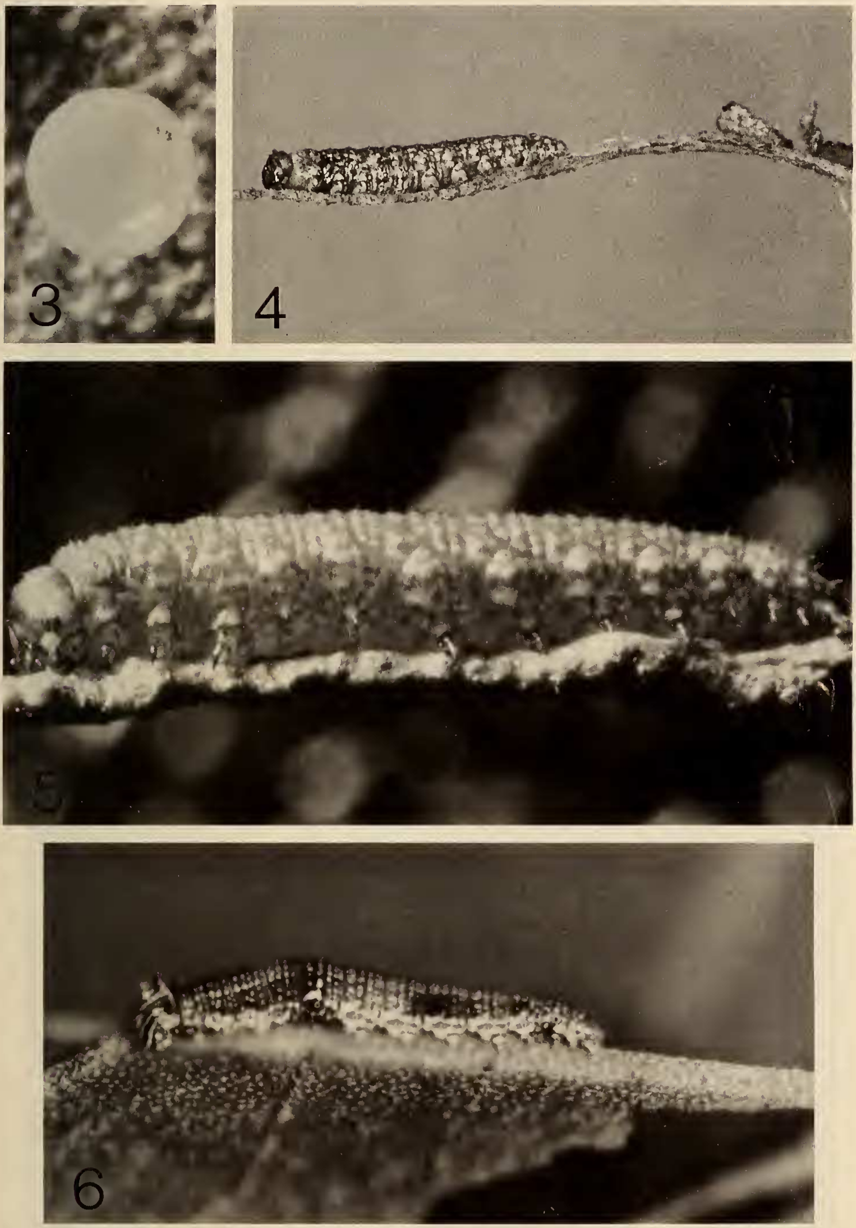
Fourth Instar (Fig. 7). Length 14–24 mm (n = 301). Head similar to third instar, with dark stripes more pronounced, scoli resembling antlers, and chalazae all over head. Body brownish green, with dark brown subdorsal stripes following second and third thoracic segments, turning dorsal and joining to form a broad dorsal band across the first and second abdominal segments; fourth through tenth abdominal segments also with dark brown subdorsal stripe; third abdominal segment entirely green. Hump on second abdominal segment more conspicuous than in previous instar. Duration approximately 7 days (n = 83).

Fifth Instar (Fig. 8). Length 20–28 mm (n = 273). Remarkably distinct from previous instars. Head green; scoli large, Y-shaped; chalazae present in greater density. Body bright green, with black dots on dorsal and lateral surfaces of all segments; second, fifth, and seventh abdominal segments with reddish hazel subdorsal stripes. Duration 8–15 days (n = 45).

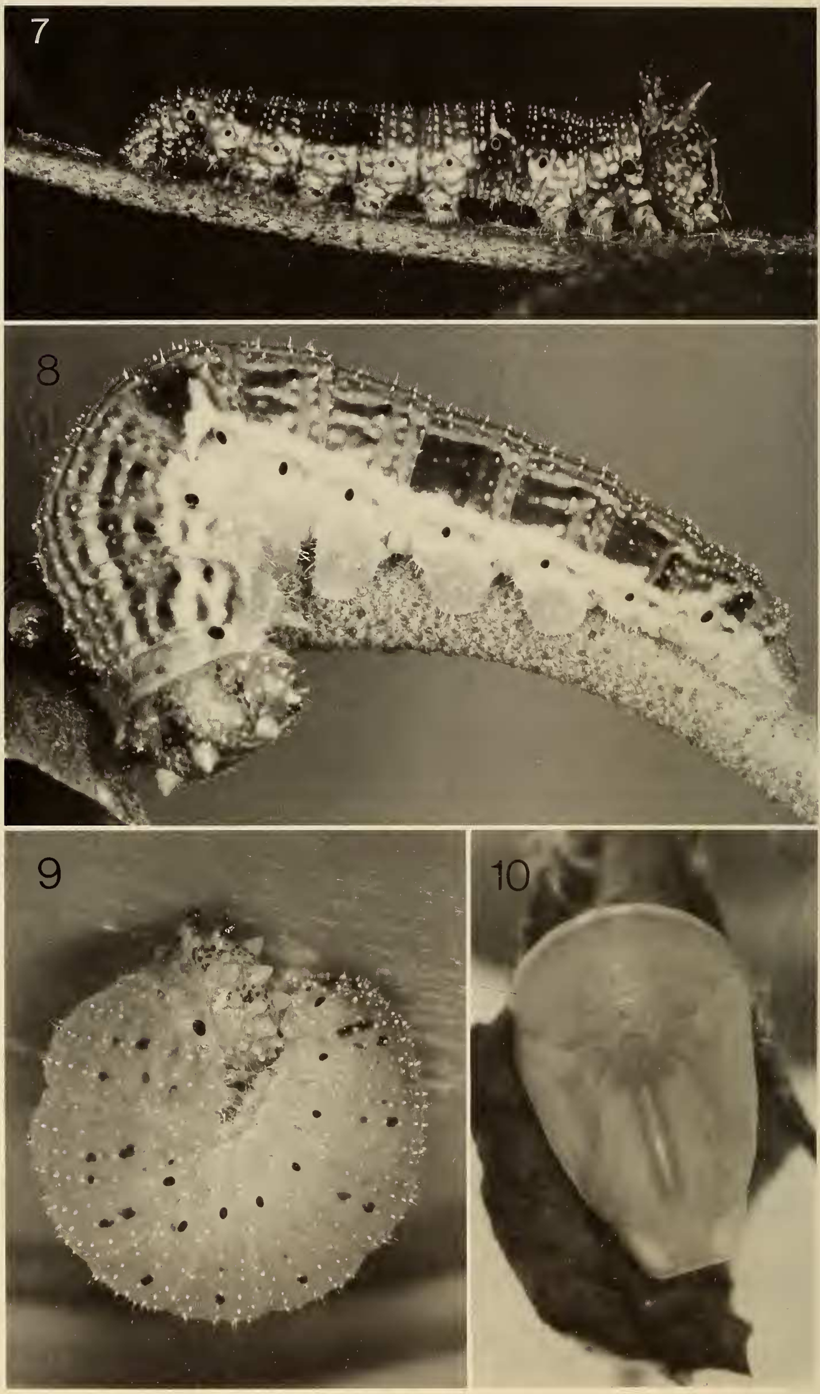
Pre-pupa (Fig. 9). Green, curled horizontally rather than vertically as in other nymphalids, and appressed to its support. Duration 2 days (n = 12).

Pupa (Fig. 10). Green, naked; dark cremaster attached to white silken pad. Duration approximately 12 days (n = 12).

The duration of the early stages in the field requires 50–60 days, accounting for individual variation. The pattern of development of *Anaea ryphea* is similar to that described for *Anaea* (*Zaretis*) *itys* on



FIGS. 3–6. Early stages of *Anaea ryphea*. **3**, Egg on *Croton billbergianus* leaf. **4**, Second instar larva with frass chain. **5**, First instar. **6**, Third instar larva.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Casearia nitida (L.) Jacq. (Flacouidaceae) (Muyshondt 1973); for *Anaea* (*Consul*) *fabius* Doubleday on *Piper tuberculatum* Jacquin, *P. auritum* H.B.K., and *P. umbellatum* L. (Piperaceae) (Muyshondt 1974a); and for *Anaea* (*Memphis*) *pithyusa* on *Croton reflexifolius* H.B.K. and *C. niveus* Jacquin (Euphorbiaceae) (Muyshondt 1975b), all of which were reared in the laboratory from field collected eggs. The eggs of the four species (including *A. ryphea*) are similar, and instars show minor variations. Duration of development is slightly shorter in *A.* (*Zaretis*) *itys* and *A.* (*Memphis*) *pithyusa*, and longer in *A.* (*Consul*) *fabius*. It is likely that the differences observed in the laboratory also would be present under field conditions. *Anaea* (*Zaretis*) *itys* differs from the others in that it does not build a leaf roll. Instead, it remains at the tip of the leaf until the pre-pupal stage. In all four species, the pre-pupae curl horizontally instead of vertically as in other nymphalids, and hang straight down only after pupation. Ramos (1984) described the pre-pupa of *A. troglodyta borquenalis* as different from these four species—it is the only one that curls vertically.

In addition to the species discussed above, the early stages of *Anaea eurypyle confusa* Hall (Muyshondt 1974b) also are similar to those of *A. ryphea*. Both use species of *Croton*, and the eggs and larvae are similar. There are slight differences in head sculpturing and body color of the larvae, and in color and shape of the adult's wings.

The life history information presented above on *A. ryphea* was collected during extensive field observations. The animals in my study were allowed to remain under natural conditions in contrast to the laboratory conditions of the other studies cited above. This is one of the reasons for the dramatic decrease in numbers of observations from one instar to the next, which more accurately reflects the fate of natural populations in the field. Only the pre-pupa and pupa stages had to be observed in the laboratory because fifth instar larvae would have been lost when they left their plants to pupate. No pupae were ever found on or near *C. floribundus* in the field.

Variations in rearing conditions can affect the ultimate form of the adult in species with seasonal forms. This was studied by Riley (1981, 1989) in *A. andria*. So far, no seasonal variation has been observed in *A. ryphea* in the field, although males exhibit considerable variation in the color and shape of the wings.

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FIGS. 7–10. Early stages of *Anaea ryphea*. **7**, Fourth instar larva. **8**, Fifth instar larva. **9**, Pre-pupa. **10**, Pupa.

Herbivory and Associated Fauna

Anaea ryphea larvae seldom were seen eating the lowest leaves (old and damaged), and they never fed on apical leaves. Other herbivores also were observed on the intermediate portions of the plants. One species of cricket (Orthoptera: Gryllidae) ate patches from the leaves giving them the aspect of lace; one species of beetle (Coleoptera: Chrysomelidae) was observed eating the petiole; and one species of true bug (Hemiptera) appeared to be feeding on the petiole. Larvae of *Hypna clytemnestra* Cramer (Nymphalidae) are common on *Croton floribundus,* frequently outcompeting *A. ryphea* with their ability to defoliate small plants. There also is a species of aphid (Homoptera: Aphidae) that uses *C. floribundus.* Individuals aggregate on the undersides of leaves, and as a result, the upperside becomes dotted with white spots.

A leaf-mining microlepidopteran was taken to the laboratory for rearing, but all individuals died before pupation; hence, identification was not possible. The mine follows the edge of the leaf and when that area is used, the larva turns toward the central part of the leaf following the central vein, never crossing it. *Pheidole* ants (Hymenoptera: Formicidae) wee seen predating upon eggs of *A. ryphea* (n = 10), but were never observed interacting with the larvae.

In addition to those species mentioned above, a variety of other insects and spiders were seen regularly on *C. floribundus,* but not feeding on it. Some individuals of *C. floribundus* produce globs of a translucent gum, usually close to the apical leaves, that perhaps serve as a mechanical defense against some herbivores.

The practice of leaving the midvein and secondary veins intact, as exhibited by *A. ryphea,* appears to represent a feeding strategy described for other species of Lepidoptera (Compton 1987), and differs from the strategy of those species that cut the midvein to prevent toxins from getting to the portion of the leaf to be consumed. The former strategy allows the larvae of *A. ryphea* to avoid contact with the latex that *C. floribundus* produces, which suggests that they are incapable of detoxifying or storing high concentrations of this substance. *Hypna clytemnestra* and the leaf-mining microlepidoptera reported from *C. floribundus* also avoid the midvein, although the former may eat secondary veins. This type of behavior has been interpreted as an important step toward a disguise for these larvae (Hingston 1932) which add pieces of leaves and fecula to the midvein to improve the resemblance of the substrate to their body (Fig. 4). Such a behavior may reduce the level of predation.

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